XXI. *On the Ovulum of* Santalum, Osyris, Loranthus *and* Viscum.

By William Griffith, *Esq., F.L.S. &c. &c.*

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In two papers which have been honoured by places in the Transactions of the Society*, I detailed, as well as I was able, what appeared to me the most striking peculiarities presented by the ovula of *Santalum*, *Loranthus* and *Viscum*; and I was enabled to point out some novel and interesting facts connected with the ovulum, such as the protrusion of the embryonary sac beyond the apex of the nucleus, and the formation of the embryo outside the nucleus. I was also led to infer the possibility of the reduction of the ovulum to its innermost coat, the embryonary sac; and to state that the ovarium of *Loranthus* was solid, and that its ovulum, as well as that of *Viscum*, was formed subsequently to the occurrence of fecundation.

In the present attempt I have, I believe, been able to supply many of the large deficiencies of the papers alluded to; to correct, I trust, some important mistakes; and to extend my inquiries to another genus of the natural family *Santalaceæ*. In extenuation of so much addition and correction to *Santalum*, and especially to *Loranthus*, I consider it my duty to the Society to state that the original observations on *Loranthus* and *Viscum* were made by a very inexperienced observer, that those on *Santalum* were not only similarly defective, but were interrupted by severe illness, and that the manuscripts were prepared during a short period between convalescence and a hurried departure for Assam; so that the papers, as they now stand in the Transactions, must have been greatly cleared from obscurities and inaccuracies by the knowledge and friendly care of those who honoured me by superintending their printing.

It will be seen by referring to the sketches, that the materials from which

* Vol. xviii. p. 59 and p. 71.

this paper has been drawn up, have been, with the exception of *Viscum*, some months in my possession. But I wished particularly to re-examine that genus, and to examine other species of *Loranthus* than the two on which the remarks concerning that genus have been founded. I could now extend the inquiry to two or three species of a Santalaceous genus closely allied to *Osyris*, differing chiefly in its quinary flowers and lobed albumen; to a plant which would belong to the "Genera Santalaceis affinia; fructu supero diversa," of the great Mr. Brown's 'Prodromus'; and I believe to genera such as *Olax* and *Ximenia*, the affinities of which do not appear to me to have been precisely determined. But I am compelled to come to a temporary conclusion of the inquiry, which now requires a determinate knowledge of the origin of the ovulum, or rather of the placentæ; and I reserve the matters, above alluded to, to be added to an account of the *Santalaceæ* and the allied families existing in my herbarium.

§ 1. Santalum.

My subsequent observations on *Santalum* have been directed to the following points, viz. the origin, structure and limits of the embryonary sac; the relations of the *boyaux* with its apex; and the origin of the embryo.

With regard to the first, I find that the protrusion beyond the apex of the nucleus takes place long before the opening of the flowers or anthers; that at the earliest periods at which I have been able to ascertain its existence, it presents itself as a membranous tube of nearly equal diameter, the exserted part being rather longer than the ovulum; and the included part apparently originating from the base of the ovulum, beyond which it does not appear to be extended posteriorly.

When the flower-bud is half developed, the embryo-sacs will be generally found to have attained nearly their full length in regard to the outside of the placenta; and with reference to the inside of this organ, they have undergone a remarkable modification, consisting in their extension backwards and upwards beyond the base of the ovulum towards the axis of the placentæ. The apex of the sac appears up to this period to be quite simple. The enlargement of the part near the apex of the nucleus has commenced; this I have throughout called the bulb or bulbous portion.

The changes that occur in the sac antecedently to fecundation consist in

the deflection of the posterior extension of the sac in the direction of the axis of the placenta, and in the appearance of cellularity and division of the apex. The contents likewise appear to undergo some changes, but these are limited to the apex, and seem to consist of a sort of condensation, and irregular and variable division, of the grumous matter.

At the period of expansion of the flower, the posterior extensions will be found to have reached nearly to the base of the placenta. Their terminations in this direction are in *culs de sac*; there is a tendency to division and irregularity of outline of all the included part, not even excepting that within the ovulum itself. The contents seem, with the exception of the part within the ovulum, to be chiefly grumous matter*, and this is again chiefly limited to the termination.

The apex appears at this period to have several (from 3 to 5) connivent tooth-shaped lobes, divided, as it were, from each other below the middle by rather conspicuous fissures. (Tab. XVII. fig. 1.) The contents, which are grumous matter and largish granules, in the more perfect examples occupy the whole of the apex, tapering below gradually into a line. The cavity of the sac is at this time continuous, the contents passing on pressure freely throughout. Iodine at this period causes the coagulation of the contents, which then appear like a brown club-shaped coagulum studded with granules, the upper end of which is partially or entirely divided from the lower, is much less or not at all granular, and is occasionally lobed and marked with a line down the centre.

At or about this time, if the bulb be examined, it will be found to present traces of a convex septum towards its lower part, and very soon afterwards traces of an additional septum, or perhaps cell of excessive fineness, are detectible above this.

The changes immediately incident on the application of the *boyaux*, which may be traced *upwards* to the stigmata, consist in the appearance of a vesicle within the apex, and the coagulation of the contents.

The tubes which descend from the stigmata, and which are fairly, I think,

* By grumous matter I mean that particular semi-opake, mucilaginous-looking matter, in which no granules are detected, and which under the microscope resembles the appearance of a solution of gamboge. It has no proper form or distinction of parts.

assumable to be pollen tubes, adhere most intimately to the apices of the sacs; generally one, sometimes more, will be found adhering. By varying the modes of examination, I acquired the conviction that the pollen tube passes down between the connivent teeth and enters the apex of the sac, when it expands into the vesicle just mentioned. (TAB. XVII. fig. 4, and especially fig. 6.)

This vesicle contains grumous molecular matter. On reaching its full amount of expansion, which is considerable, the free end will be found in direct communication with the coagulum, which forms an uninterrupted line as far as the convex septum; its upper end tapers into a neck, which corresponds with the axis of the teeth and with its sides; but to an unequal and incomplete extent, dense grumous matter will be seen to be in contact.

The coagulation of the contents is universal; it is most distinct in those that are to be abortive, in which it forms a flattened club-shaped line, studded here and there with a few large granules, almost all of which do not fail to disappear from the fertilized one.

The abortive tubes undergo no further change; the fertilized ones soon present cellularity of the bulb and nucleary aggregation of the contents of the neck, which subsequently also becomes cellular. (TAB. XVII. fig. 7.)

The cellularity of the bulb is always in advance, and even when it has attained a considerable size, the upper or tubular part presents only the first steps to cellularity, aggregation into nuclei, and then the division of these. The direction of the cellularity in this part appears irregular, but generally I have observed it to be most developed towards the vesicle and towards the bulb, and least in the intermediate part. If the bulb be examined about this period, it will be found that the cells have, as it were, extended downwards over that part of the sac beneath the septum, and that the whole of the bulb and tubular part is easily separable from this, which, when detached, presents an entire globular head strikingly similar to that of *Osyris*.

The cellularity continuing to increase, finally occupies the whole sac above the line of separation, and in the meantime the lower free end of the vesicle will be found to present traces of internal subdivision, preceded by the aggregation of its contents into nuclei. (TAB. XVII. fig. 9.) The next process consists in the development of cells from its lower free end, and from these again other cells are developed, forming a cylindrical mass of lax nucleary

cellular tissue, which reaches to a considerable length before the more condensed structure of the embryo becomes visible.

As the cellularity of the original sac increases, all traces of its original structure disappear, and it becomes a cellular mass, divided completely into as many parts as there are component cells. (Tab. XVII. figs. 10 and 11.)

During these changes the posterior extensions of the sacs have become longer and more divided, and they penetrate to a considerable distance below the placenta into the white cellular substance constituting the ovarium, forming extensive relations of superficies with it. (Tab. XVII. fig. 8.)

It is perhaps unnecessary to trace the development further. I have ascertained the existence of the vesicle, in the state I have just mentioned, when the embryo is half-developed. It appears, perhaps, throughout to have relations to the lax cellular mass of the embryo a good deal similar to those it originally bore to the grumous molecular contents of the embryo-sac.

It will be seen from this that my present statements regarding *Santalum* differ considerably from my previous ones, with regard to the apex of the sac, its posterior extension, the subsequent separation of continuity, and its relations with the *boyaux*.

With regard to the first point of difference I have nothing to offer; that which I have now described as the appearance of the mature apex requiring no nicety of observation. To the extension posteriorly and the interruption of continuity I was led by *Osyris*; otherwise, from the parts remaining in contact, it is liable to be overlooked. The last correction has resulted from very extensive repetition (for the "blending" is occasionally apparent), and from improved means of observation*.

* I may here mention, that the observations on *Santalum*, *Loranthus* and *Viscum* were made almost exclusively with one of Mr. Ross's compound achromatic microscopes, the object-glasses of which were supplied to me in 1836, and have respectively $\frac{1}{4}$th and $\frac{1}{16}$th inch focal distances. Verification, when necessary, was made by excellent triplets of various powers by the same eminent optician. I have also had the advantage, as occasions offered, of examining some of the minuter points by the superb Rossian microscope of Mr. Grant, to whom I am indebted for direct proof of the engagement of the pollen tubes in the apex of the embryo-sac.

My compound microscope, though now of some years' date, is fully equal to any triplet in my possession in defining and penetrating powers; and as I have from repeated comparison acquired confidence in it, and as it possesses such obvious advantages over any modification of the simple microscope, I seldom now use any other. The observations on *Osyris* were made almost entirely by simple microscopes; all the minuter points being observed under excellent triplets of $\frac{1}{20}$th and $\frac{1}{30}$th inch focal distances.

§ 2. Osyris Nepalensis.

The ovula of this plant are cellular productions from the lower part of a conical cellular placenta, imbedded in a small cavity a little above the centre of the ovarium; this cavity communicates freely with the stigmatic canal by a narrow line or slit. (Tab. XVIII. fig. 1.) Before the expansion of the flower the outlines of these ovula are continuous, and they present all the appearances characteristic of ovula reduced to nuclei; they are oblong, cellular, homogeneous bodies, curved upwards or laterally. (Tab. XVIII. fig. 2.)

At the period of expansion of the flower, but before any evident action of the pollen on the stigmata, an oblong sacciform body crowded with granules will be found protruding from the apex of the ovulum; this, which is very short, may be traced into the ovulum, within which it becomes narrowed, as far as its base. (Tab. XVIII. fig. 3.)

If, after the action of the pollen on the stigmata is apparent, the ovaria be carefully opened, very fine tubes will be seen in the canal of communication or stigmatic canal, which on reaching the apex of the placenta pass down over its surface, and establish immediate relations with the ovula; possibly with all, but generally, as it has appeared to me, with only one, or at most two. (Tab. XVIII. fig. 4.)

The relation established consists of a very firm adhesion with the apex of the protruded sac. No pressure or traction is sufficient to disunite them; occasionally the membrane of the descending tube or *boyau* appears blended with the protruded sac, occasionally appearing to expand upon it in a somewhat bulbiform mode. (Tab. XVIII. fig. 5.) At this period the protruded tube, which I consider to be the embryonary sac, will be found to present a continuation backwards beyond the base of the ovulum into the placenta, on reaching the central line of which it becomes deflexed, passing down to a considerable distance in the centre of the tissue which corresponds to the central line of the ovarium, and which contains the vascular supplies for the placenta?? (Tab. XVIII. fig. 4.)

The next stage of development has presented to me the appearance of a small cellular mass, apparently occupying the place of the exserted part of the embryonary sac, and generally, perhaps, presenting on its apex traces of very short filaments. This cellular appearance arises from the deposit, if I may be

allowed the use of the expression, of minute and laxly-formed cells, crowded with molecular matter, on the surface of the protruded part of the embryonary sac, which may be freed by pressure from these cells, when it will be found to retain its original sacciform appearance. (Tab. XVIII. figs. 6, 7, 8 and 9.)

To this cellular body all the subsequent changes relating to the embryo and seed are confined. It continues to enlarge by the addition of cells *upwards*, and all traces of the filaments seem rapidly to disappear.

At the period of the appearance of the embryo itself, which takes place about the time when the cellular mass, now young albumen, equals in bulk the placenta, the embryonary sac will be found to present the appearance I have above attempted to describe, and except in the disappearance or coagulation of its molecular matter, it has undergone no change. (Tab. XVIII. fig. 10.) It is detectible unchanged in the placenta of the ripe fruits long after this body appears to exercise any function, at least judging from its withered and dried state.

I have not detected the embryo before the cellular mass has reached a considerable size. In the earliest stage at which I have seen it, it consists of from 3 to 5 cells growing from the surface of a single one a little within the apex of the cellular mass. (Tab. XVIII. figs. 10 and 11.)

The changes in the young fruit, besides mere increase of size, consist first in the dislocation or breaking up of that part of its cellular tissue immediately around the placenta; this goes on rapidly, the cells being found either quite freed from their original relations or grouped in small masses. (Tab. XVIII. fig. 12.) When it has reached to a considerable extent, it is accompanied by an induration of the circumference of the same tissue, the whole of which I imagine corresponds to the ovarium. The induration and dislocation go on increasing; they are followed at an advanced period by the baccation of the tissues between the cutis and the hardened portion or outer surface of the drupe, the whole of which baccate portion may be supposed, in accordance with generally received, but not improbably erroneous opinions, to represent the adherent tube of the calyx and staminal apparatus.

In the ripe fruit, the originally very thick cellular ovarium will be found to consist of an almost bony outer coat of some thickness, and an irregular lining of film, the *débris* of the dislocated tissue. The cavity of the drupe is

occupied by a coniform mass of albumen, on one side of and beneath which will be found the remains of the placenta and its stalk, now reduced to a flattened body, covered with irregular cellular tissue. The embryo does not correspond exactly to the axis of the albumen. (TAB. XVIII. fig. 12*g*.) Minor changes consist in the growth of oblong, clavate cells from the surfaces of the barren ovula, and probably in the absorption or breaking up of the tissue of the nucleus of the fecundated ovulum.

§ 3. LORANTHUS.

The examination of several species of *Loranthus* has satisfied me that an ovarial cavity does exist throughout the earlier stages of development, however obscure it may become subsequently, and that the ovula do exist before fecundation has been effected.

For the appearance of that cavity I refer to TAB. XX. fig. 1. of *Loranthus bicolor*; and as the subject requires revision, more especially regarding the nipple-shaped process, represented as occupying the fundus, I shall content myself with describing the ovula*, their relations with the pollen tubes, and the changes consequent on the occurrence of these.

In all the species I have examined the ovula consist of closed membranous sacs, the upper extremity of which is rounded and generally dilated. Their contents are grumous matter and some fluid, the former being generally crowded in the head of the sac. (TAB. XX., *Loranthus bicolor*, figs. 4 and 5.) The extent of these sacs is in all cases considerable, but still varies remarkably; the variation appearing to be connected with a remarkable modification in the situation of the albumen and of the embryo throughout the earlier stages of its development. I have not in any instance hitherto been able to observe that they had any *definite* relations with the nipple-shaped process of the fundus. Their number is perhaps generally 6; and a transverse section shows them to be arranged regularly enough round the obscure cavity in the axis of the base of the flower.

In one of the modifications above alluded to, of which *Loranthus globosus*, Roxburgh, is an instance, these sacs are confined to the part which is de-

* Of the origin of these ovula or the direction of their development I have not ascertained anything sufficiently precise.

scribed as "ovarium" (Tab. XIX. fig. 1); in the other, exemplified by *Loranthus bicolor* of the same author, they extend a long way up the canal of the style, reaching not unfrequently to within a short distance from the stigmatic surface itself.

In both modifications, after obvious action of the pollen on the stigma, filaments will be found adhering to the heads of the sacs, into which they penetrate, becoming dilated within the dilated apex of the sac, and constricted in its constricted part; not, however, to their limits or diameters previous to their penetration (*L. bicolor*, Tab. XX. fig. 6; *L. globosus*, Tab. XIX. fig. 2): they run down throughout the whole length of the sac, being always, so far as I have seen, while within this organ, two in number and in close apposition to each other. In *L. bicolor* they appear to run without interruption of continuity (Tab. XXI. fig. 2) almost to the very end of the sac; in *L. globosus* they have generally appeared jointed immediately above that part of the sac in which the albumen becomes developed. I cannot state positively whether these tubes, or their *similar* continuations, pass out through the lower end of the sac, but growths from the ends of these, shorter, of larger diameter, and subsequently of increased number, certainly appear to do so.

In that modification of sac which does not extend beyond the so-called ovarium, the penetration of the tubes appears almost immediately associated with the appearance of grumous nuclei in a particular part of the sac, which nuclei, soon becoming invested with proper membranes, form the cellular tissue of the young albumen. But in the other modification this is not the case, but the analogous cellular tissue is developed *from* the ends of the sacs, and within the mass there formed the continuations of the pollen tubes will be found. (Tab. XXI. fig. 3.) And it is remarkable, that whereas in the first modification the sac retains its original simple membranous nature, unless pollen tubes have penetrated into it (*L. globosus*, Tab. XIX. fig. 4), yet in the second, each sac appears to have to some extent independent powers of growth, inasmuch as cellular tissue is often produced from their ends without any such penetration having taken place. (*L. bicolor*, Tab. XX. fig. 7; Tab. XXI. fig. 1.)

In *Loranthus bicolor* the continuations of, or growths from, the pollen

tubes do not reach any great length before they pass, as it were, into the tissue of the young embryo, this never appearing to be altogether external to the albumen even in its very young state. But in *Loranthus globosus* the case is widely different; the continuations of the pollen tubes are greatly extended before the proper tissue of the embryo appears to be developed. (TAB. XIX. figs. 3 and 4.) In consequence of this extension, they assume a variously bent or even contorted appearance; for the sacs themselves being of the same length as the cavities in which they are inclosed, and the tissues of the base of the central part of the ovarium being dense and not admitting penetration, the growths alluded to are necessarily disturbed in direction. (TAB. XIX. fig. 4.)

At a variable distance in *L. globosus*, but almost immediately in *L. bicolor*, the growths from the pollen tubes meet and become united, forming either immediately or mediately the ground-work of one embryo (*L. bicolor*, TAB. XXI. fig. 3; *L. globosus*, TAB. XIX. figs. 4 and 7); but it is proper to observe, that in *L. globosus*, at least, a tendency towards separation of the growths of the pollen tubes after junction is not unfrequent. (TAB. XIX. fig. 4.) The same union affects the young albumina of both species, occurring however earlier in *L. bicolor*.

The embryo of *L. bicolor* presents nothing particularly worthy of notice in its further evolution; it presents throughout no great deviations from the ordinary relations existing between albumen and embryo. (TAB. XXI. fig. 7.) In *L. globosus* it is only at a late period that it becomes inclosed in the ordinary manner in the albumen (TAB. XIX. fig. 4), through the constant tendency of the embryo to be developed in a line with the axis, the pressure opposed to it by the density of the tissues of the base of the flower, and the extension downwards of the growth of the albumen. When mature, the embryo presents its huge radicle projecting beyond the upper surface of the albumen. (TAB. XIX. fig. 6.) I have to add, that in this species the development of the young albumen does not, for some time at least, affect the appearance of the pollen tubes; these may be seen, under pressure, in their original form even when the albumen has reached to a considerable size.

The above observations I consider as going no further than to establish the existence of an ovarial cavity and of the ovula, independently of fecundation;

the percursion of the ovula by the pollen tubes; the existence of at least two distinct types of development in the genus*; the formation of one mass of albumen from the albumina of several ovula; the *exteriority*, if I may so express myself, of the embryo from the ovulum; and its concentrated formation.

§ 4. Viscum.

I have not yet had an opportunity of re-examining a species of *Viscum*, presenting the organization of that from Mergui, on which my first remarks were founded. The examination, however, of two species of another type†, though remarkably different in habit from each other, has satisfied me not only that the reduction in the parts of the ovulum is of the same degree as that occurring in *Loranthus*, but that the ovulum equally exists before fecundation, and that the phenomena consequent on the occurrence of this present little if any peculiarity, even as regards a retardation of the usual effects.

The circumstances do not now appear to me to present sufficient variety to induce me to enter into detail, such as I have thought requisite with regard to *Loranthus*, *Santalum* and *Osyris*, particularly as I am not now able to enter into the question of the origin of the sac (ovulum) and the nature of the parts by which it is surrounded. I consider it, therefore, sufficient to state that the ovulum, which I consider to be reduced to an embryonary sac, exists before fecundation as a clavate membranous closed simple sac, containing fluid matter with some grume towards its apex (Tab. XXI. figs. 5 and 6); that after fecundation has occurred, its apex will be found to present traces of interruption of continuity, and to be occupied partly by a vesicle, which I assume to be derived from the inner membrane of the pollen, and to be the "anterior extremity" of the pollen tube; that the changes consequent on the penetration of this consist first in the development of cellular tissue in the sac, being the first step in the formation of albumen (Tab. XXI. figs. 7 and 8), and that this is subsequently accompanied with the occurrence of cellularity in the vesicle and its

* I am not yet certain whether these two types are so far connected with external form as may enable me to propose more natural subdivisions of the genus than those at present adopted.

† M. Decaisne in a letter alludes to the possibility of there being two distinct types of organization of the male flowers of *Viscum*. Reserving this, I can say that there certainly are as regards the female; and these, I hope, may be of some use in determining subdivisions and species. At present, nothing can be more inefficient than the characters of the species in Decandolle's 'Prodromus.'

conversion into the embryo. (TAB. XXI. fig. 9.) And this is I think its only anomaly, that is, comparing it with *Santalum*, and more especially with *Loranthus**.

In connexion with these details, I venture to remark on the following points:—

1. Solidity of the ovarium, and the appearance of the ovulum after fecun-

* My paper on *Viscum* appears, I am sorry to say, to have been generally misunderstood. In a letter dated April 1839, M. Decaisne states that the development of the ovula of *Viscum album* is like that I had described as occurring in *Loranthus*, and that the development of the same part in the Mergui *Viscum* appears identical with that of *Thesium*. In the translation of his memoir on Mistletoe, it is said that in that same species three ovula are detected in each cell on a central support.

These discrepancies are by no means confined to the ovulum; they extend to the fibrous covering of the seed.

It appears to me that the only similarity in our observations is to be found between *Santalum* and *Thesium*; for the whole of his observations on the female parts of *Viscum album* differ from those which I made on a tropical species of the same genus. Between M. Decaisne's inferences and my own there is little analogy; for while, according to him, *V. album* presents no anomaly in its ovulum beyond reduction to a nucleus, I was led to the conclusion that the anomalies, affecting this genus, at least as exemplified by the Mergui species, are of a more remarkable nature.

When I was occupied in 1834–35 by the structure of *Viscum*, the question of the nature of the part, which I called nipple-shaped process, had occurred to me, although in my account I did not enter into any detail regarding it. My assumption of its being rather analogous to a placenta was founded on the eccentricity of the sac, which I consider the sac of the embryo.

I knew of no instance in which the embryo sac had not a definite relation to the axis of the nucleus, or in which it arose from the surface of that body. I therefore described the part in question as a nipple-shaped process, avoiding, in the imperfect state of my knowledge, all speculation as to its nature. Although a good deal dismayed by my blunders regarding the solidity of the ovarium of *Loranthus*, I am still inclined to adhere to the other inferences therein contained: for although in the description of fig. 5. (by mistake 4.), TAB. X., vol. xviii., it is inadvertently stated that the ovulum is reduced to a nucleus, what I believe to be its true nature is elsewhere distinctly alluded to.

The structure of the Mergui *Viscum*, as there detailed, is an obvious approach to that of *Santalum*. And I should not be surprised, from my greater experience of *Santalum* and acquaintance with *Osyris*, if it be found to approach so closely as to differ in little except in the absence of a nucleus; the constant browning of the tissue of the placentæ along the line of the posterior extension of the embryonary sacs in those genera leading me to suspect that something of the same nature occurs in *Viscum*. The occurrence of two such dark lines with the development of only one sac still further points out the importance of studying every species of this genus: for this would seem to indicate the existence of the sacs or tubes in the placentæ prior to their exsertion; a fact of considerable importance, and one which, if established, would considerably modify my ideas of the nature of these particular placentæ.

dation, or rather, after the action of the pollen upon the stigmatic surfaces.

2. The reduction of an ovulum to the nucleus or to the embryonary sac.
3. The embryonary sac.
4. The origin of the embryo.

1. *Solidity of the Ovarium, &c.*

The only evidence in favour of the occurrence of a solid ovarium that remains uncontradicted is, so far as I know, that of M. Decaisne on *Viscum album*, and that derivable from some casual observations made by myself early in 1838 on a Himalayan species of the same genus; and the evidences in favour of the occasional appearance of the ovulum after the first parts of the process of fecundation have been accomplished, are drawn solely from my observations on the Mergui *Viscum*, and those of M. Decaisne on the European plant. For having erroneously stated the existence of so remarkable an anomaly in *Loranthus*, I cannot hope to escape censure on the grounds of the obscurity of the appearances; these, on the contrary, ought to have made me more than ordinarily careful in the manner and amount of investigation: for there is, perhaps, nothing more constant than the existence of a cavity in the pistillum, nor is its absence compatible *throughout* with the very general, and perhaps universal rule, regarding the composition of a pistillum from one or more involute carpellary leaves.

It is easy to conceive a pistillum without any very manifest cavity; for the space, which must exist from the disposition of its component parts, may be filled by an extension of the placentæ, or the margins of the laminæ of those component parts, and indeed by several other modes of extension of its inner surface. But the solidity which I so prematurely announced as existing in *Loranthus* was of a very different nature, and could not be reconciled to the idea of a pistillum, which I have been led to adopt. The anomalies of the mere pistillum of *Loranthus* I at present consider to be confined to the obscurity of the cavity, particularly as connected with obscurity of the placentæ. I have, however, seen in *Loranthus bicolor* appearances which lead me to suspect that much still remains to be observed, not only as regards the conical eminence from the fundus of the cavity, but as regards the true limits of the ovarium.

I have not been able to find any such ovarial cavity in the two species of *Viscum* I have lately examined; but my inquiries have not been made at a sufficiently early period, on which *Loranthus*, I think, shows so much depends. Further observations on *Viscum* will, I almost feel convinced, show that an obscure ovarial cavity similar to that of *Loranthus* exists: for in addition to the strong doubts that must arise from any apparent infraction of a general law, M. Schleiden has stated that in *Viscum album* there is a nucleus, and consequently an ovarial cavity.

The late appearance of the ovulum does not, I think, present so remarkable an anomaly as the solidity of the ovarium, unless it can be shown that the development of the ovulum results from the action of the pollen. For there are many instances, I think, of considerable irregularity in the degree of development of the ovulum at the period of expansion of the flower; and the rather later appearance of the ovula of *Loranthus* is, it appears to me, in exact accordance with the nature I have ventured to assign to them; the embryonary sac being the last part of the independent ovulum that is formed, not being evident, perhaps occasionally, until the action of the pollen on the stigma has taken place.

From M. Decaisne's description of the ovulum of *Viscum album*, which appears to agree tolerably well with that of an Himalayan species, it is, I think, evident that in the earlier stages of its development it may defy observation, since at one period it would seem to consist of nothing but a single cell, scarcely, if at all, distinguishable from the cells composing the surrounding cellular tissue.

The apparent determination of the development of the ovulum by fecundation, and the lapse of time mentioned by M. Decaisne as intervening between the two processes, appear to me very remarkable. The first would seem to infer the absence of any palpable pre-existing punctum on which the male influence is to be exercised. And if the development of the ovulum be really found to be the effect of the action of the pollen, it appears to me that considerable light will be thrown on those Acotyledonous plants, which, though apparently furnished with male organs, have no evident apparatus analogous to a pistillum; because, if the male influence of *Viscum album* be so exercised as to cause the development of the embryonary sac, followed by that of the

seed from a cell of the parenchyma of a part of the ovarium, we need not be staggered by assuming that the male influence of *Anthoceros*, and possibly of Ferns, causes the development of the organs of reproduction from the parenchyma of the frond at a distance from the point to which the male influence is first applied. And this argument will, I think, be a good deal strengthened if the usually-adopted notions of an "*ovarium inferum*" be so explained by investigation as to refer the part of the ovarium of *Viscum*, in which the embryonary sac becomes developed, to the axis, which, I believe, is M. Schleiden's view of its nature.

The second, even if it be established as resulting from the excessively slow travelling of the end of the pollen tube, will tend to show that there need be nothing at all contemporaneous between the occurrence of fecundation, as shown by the stigmatic changes, and its results. And this, taken in conjunction with the fact that the ovulum of *Osyris* does not enter into the composition of the seed, and is unchanged by fecundation, may, I think, be legitimately made applicable to the explanation of the phenomena presented by Mosses subsequently to fecundation. I think also that it materially weakens the arguments which, in conformity with perhaps arbitrary notions of the necessity of immediate relations as to time in the fecundation of these plants, require the sexes to be sought for in the capsule*, and those which with more reason might have been urged from the ovulum itself suffering comparatively no change.

2. *Reduction of an Ovulum to the Nucleus.*

The non-development of either of the ordinary integuments of the ovulum, that is, the reduction of this to the nucleus, was, so far as I know, first observed by M. Adolphe Brongniart in *Thesium*; and this is the only point on which the observations of this distinguished botanist agree with the later ones of M. Decaisne†. This sort of reduction or suppression is now known not to be

* See Mr. Valentine "on the Development of the Theca and on the Sexes of Mosses," Linn. Trans. vol. xvii. p. 477.

† So different are these two accounts, both of which are illustrated, that it appears evident that two observers, having one and the same object *sub oculis*, may represent it in two very different, and indeed opposite manners, or that the sports of nature are not always confined to form. If this latter be the case, my ideas of structure will be almost as much shaken as my ideas of many of the usually adopted Orchideous generic forms have been by the celebrated variations of *Monacanthus*.

uncommon: it is usually, I believe, considered to be limited to antitropous ovula; but from the consideration of *Galium*, *Callipeltis* and *Osyris*, I am inclined to believe that changes in direction affect nucleary ovula similar to those affecting more complete ovula, so permanently established by M. Mirbel*. This suppression having first been made manifest in *Santalaceæ*, it naturally became a subject of consideration whether it did not exist in similar placentations of certain other natural families, of which *Olacineæ*, certain *Verbenaceæ* and *Avicennia* are marked examples. On this subject my direct observations are confined to *Congea*; and although these are incomplete, I am led to believe that there is not any connexion between this mode of placentation and this mode of suppression. It is curious, however, that the ovula of the above instances, so far as I am acquainted with them, simulate at the period of expansion of the flower in a sufficiently marked manner the ovula of *Santalaceæ*. Of the reduction of the same organ to the embryonary sac, I believe I was the first, and am the only advocate; my reasons will be found detailed in the following section.

3. *On the Embryonary Sac.*

There appears to be little definite about the sac of the embryo, either in period of development, situation or structure†; but ordinarily it may be recognized as the sac existing within the nucleus, and as that in which the embryo is developed. I know of no positive character that can be assigned to it; for I have reason to believe that in *Xanthium* a second sac is to be found; and to say nothing of it, *Osyris* shows that the embryo is occasionally developed outside it‡.

* M. Schleiden in his memoir "on the Organization of Phænogamous Plants," Lond. and Edinb. Phil. Mag., 1838, p. 185, appears to think that in *Santalaceæ* the ovulum is an "*ovulum anatropum*," and says that he had never met with an instance of reduction to a nucleus in any other modification of this organ, although he very justly observes, that there is no reason why such may not be the case.

† See Schleiden's Memoir, *op. cit.* p. 243.

‡ It has, I believe, been supposed by some, particularly by M. Brongniart, that the embryo of *Ceratophyllum* presents a similar anomaly. But I believe it will be found that in *Ceratophyllum* and certain *Naiades* the appearances are due to a particular development of the cells of the funicle or suspensor of the embryo, in conjunction with a great degree of tenuity of the sac itself and of rapidity in its development.

Very generally it is confined to the nucleus, and so far as I know, the first notice of its *continuous* exsertion was given in *Santalum*.

Various considerations induced me to pay considerable attention to the origin and subsequent relations of this sac in *Osyris* and *Santalum*, but I cannot say that the observations have appeared to me altogether satisfactory. I am inclined, however, to believe that in their earliest stages they do not differ from the ordinary fashion of sac; neither is the extension of a single cell a modification, so far as my experience goes, generally confined to albuminous seeds, nor its degree particularly remarkable; it is in the protrusion and extension backwards that the anomalies consist.

In *Osyris* none of the means at my disposal enabled me to detect the sac in the placenta before its presence in the ovulum was ascertainable; nor did I detect any such different degrees in its extension backwards as might have been expected.

In *Santalum* I believe the sac is developed from the interior of the nucleus, first in an anterior, subsequently in a posterior direction; and this, connected with its apparent limitation at a very early period to the nucleus, and the non-extension of the sacs of the ovula in *Osyris*, which are barren, point out, I think satisfactorily, that what I have called the nucleus is in reality the ovulum: otherwise it might have been, it appears to me, an open question whether the placenta itself was not the ovulum (analogous to those which contain more than one embryonary sac), to the nucleary forms of which it has considerable similarity in the cellularity of its apex. It must be confessed, however, that apparently formidable objections to this assumption would exist in the want of a common line or point of fecundation, and more importantly still, of correspondence in direction of the sac and supposed nucleus.

The extension backwards of this sac is also, I believe, now pointed out for the first time, unless the apparatus, to which M. Decaisne is said to attribute the function of a chalaza, be something of the same nature. It first passes upwards until it reaches the axis of the placenta, or nearly so; it is then deflexed: its presence appears always to be connected with a slight browning of the tissues, with which it is in contact: subsequently it reaches a considerable distance below the base of the placenta. In *Santalum* the extension, especially the placental portion, presents an irregular surface, and throughout, but most

especially towards its termination, has a remarkable tendency to ramification. It is to be observed, also, that towards its point of growth it always seems to present minute molecular matter.

In *Osyris* this sac has presented to me uniform appearances, and is more satisfactorily observed from the extension backwards appearing to be generally confined to one ovulum.

In *Santalum*, whenever the protrusion is observed in the expanded flower, the extension backwards also presents itself. I have not observed any striking differences in length, size, &c., between those of the barren and fertile ovula. Its study is also obscured by its tendency to branching, which I have remarked within the nucleus itself; nor have appearances been altogether wanting to suggest to me the probability of the occasional union of two at least of the tubes into one.

In both genera the appearances of the protruded parts are uniform. Two striking exceptions were observed in *Santalum*, in which two tubular portions originated from one bulb; and in one case both were completely developed, suggesting the possibility, as is also pointed out by the posterior branching, that one embryonary sac may be so modified as to produce several comparatively independent embryos.

On the exact structure of the apex of the sac (in *Santalum*) in its mature state I have no direct observations to offer. I believe that the appearances are due to the presence of from 3 to 5 cells attached to the simple apex of the sac; but whether these cells are derived from the placenta, or whether they belong more properly to the sac itself, I am quite ignorant. The tendency to adhesion to the placenta, the appearance of these cellular teeth, and their not appearing to originate from the extreme apex, may perhaps be taken into consideration as arguing their placentary origin.

The contents of the sac in *Osyris* appeared to me minutely molecular, and to have agreed with the contents of the ends of the posterior extensions of *Santalum*. In *Santalum*, with similar minute molecular matter, granules of various sizes, often very large, occur, both being endowed with mobility. Iodine colours the mass of contents, before the application of the male influence, violet-blue; this is especially evident where there is any aggregation of granules, for there is even at this time a tendency to a fuscous colouring in

the grumous matter. After fecundation has occurred the coagulum is coloured fuscous, the violet tinge occasionally, but not always, affecting such of the granules as have not disappeared.

The changes in the contents of the sacs consequent on fecundation are not marked in *Osyris*, or in that portion of the sac of *Santalum* below the septum. Above this, as I have mentioned, the first change consists in a sort of coagulation, which is very evident in those determined to be barren, in which they will be found to be changed into a grumous mass, in apposition above by a broad base with the free end of the vesicle, tapering thence into a flat, often undulated line, communicating with the vesicle and with the summit of the convex septum; the line of communication being often interrupted towards this point. To the broad part of this coagulum a few of the largest granules will generally be found adhering.

The coagulation is much less marked in the fertilized sacs, and is chiefly observable from a tendency to the aggregation of the grumous matter into masses, accompanied by the complete disappearance of the larger granules. This aggregation of grumous or minutely molecular matter seems to me to constitute the prelude to the appearance of cellularity. I have been particularly struck with it in following the development of the pollen of certain plants, with which the development of the cells of the young seed of *Santalum* would appear to present curious analogies. (Vide Tab. XVII. fig. 7.)

The cellularity is first manifest in the bulb above the septum, in which situation the nucleary aggregation is of earlier occurrence and more decided appearance. The strong tendency to the first appearance of the cellular tissue at the part alluded to, is shown by the occasional occurrence of a cellular bulb and an abortive tubular portion. The last direction in which it becomes evident is in the intermediate part of the tube, but there is perhaps some little variation in this respect.

It is in the appearance of the cellularity at such a comparatively great distance from the vesicle that one of the principal anomalies of *Santalum* appears to me to consist. On this singular point I can offer no explanation, the limits of the vesicle being distinct some time after the commencement of the cellularity of the bulb. I have not been able to ascertain any tendency to such elongation of the vesicle downwards as would enable me to refer the

growth of the cells to it; neither would such an occurrence, perhaps, be consistent with the situation at which the embryo subsequently makes its appearance. In the barren sacs, appearances may often be seen of a sort of tubular communication between these remote points; but these are always partial, and always least evident close to the vesicle. This occurrence of the cellularity so remote from the end of the *boyau* is obviously analogous to what occurs in *Osyris*, if the situation of the embryo be kept in view, and perhaps may be taken into consideration in explanation of the origin of the first similar cellular tissue in that plant; and it appears to me to show that the sac in question is possessed, at least in certain instances, of higher functions than M. Schleiden seems disposed to allow.

Another remarkable anomaly in *Santalum* consists in the subsequent separation of the sac along the line of the septum, for such I believe to be the part at which the solution of continuity takes place. My observations on this point, and indeed as regards the actual structure of the bulb, when cellular, are by no means so decisive as I could have wished; this will be evident from inspection of the drawings. In general, appearances are perhaps in favour of the supposition of the formation of a globular cell from the septum, which cell forms the head of the lower part of the sac; if this is the case, it becomes completely identified with those parts of the septum from which it is supposed to originate.

This extraordinary separation is not the only manner in which a striking transition to the form of sac in *Osyris* is manifested; for the original tubular sac will at a certain, and not very late period, be found entirely incorporated with the cells, being divided into as many integral parts as there have been cells developed within it. This is remarkably different from what takes place in some other membranous embryo-sacs, in which, even in the ripe seed, the membrane continues to exist in its original entire state, forming a hyaline edge round the albumen.

At this period the similarity between *Santalum* and *Osyris* is highly remarkable, differing so much as they did in original structure; and were it not for the obvious continuity of the whole of the embryo-sac of *Santalum* at an earlier period, I should be tempted to consider the part above the septum to be of an intermediate nature, analogous to the process of the

sac in *Cucurbitaceæ*, and more remotely to the processes of the stigmata of *Asclepiadeæ*.

Osyris, independently of the extension backwards of the sac, presents great anomalies in its functions, although, as will be seen, there is a tendency to the same in *Santalum*.

Embryo-sacs, whenever they exist, are generally supposed to contain the embryo, and it is in them that all the important changes consequent on fecundation take place. In *Osyris*, however, although the sac has direct relations with the *boyaux*, no penetration or inflection appears to occur; but the cellular growths are formed, or, as they appear to be, are deposited on its convex surface; and it undergoes no change, except, perhaps, a greater amount of protrusion, due, I think, to the disappearance of part of the nucleus, and a less amount of adhesion to the cellular mass. Elsewhere, whenever an embryo-sac exists, it enters into the composition at least partially, and very generally entirely, of the seed. In *Osyris* it does not appear to do so. *Osyris* is, I think, also very remarkable from the direction in which the embryo appears, which is *towards*, not, as in *Santalum* and *Loranthus*, *from* the pollen tube, and still more so in its apparent distance from the end of the pollen tube, when attached to the head of the embryo-sac.

Application of the *boyaux* is in *Santalum* of very general occurrence, but the fertilizing effects are almost invariably confined to one sac. So far as I have examined, there are no appreciable differences between the sacs before fecundation, or in the manner or degree of application of the *boyaux*: on this considerable stress may perhaps be laid, as it appears to me to be fatal to the hypothesis of M. Endlicher, who considers the moisture of the stigma as the fertilizing substance; to that of M. Schleiden, who attributes similar functions to the embryonary sac; and to that of M. Unger, who believes that the pollen grains, when they arrive on the stigma, are already fecundated*: all of which speculations truly deserve the name of hypotheses.

Although my numerous observations have had especial reference to the point, I have not been able to show by *direct* observations that the vesicle is the end of the pollen tube, but I have no doubt that this may be done. I rely on the evidence furnished me by my friend Mr. Grant as to the absolute

* Meyen's Report for 1839 on Physiol. Bot., Ann. and Mag. Nat. Hist., No. 43, May 1841.

engagement of the pollen tube between the cellular teeth of the apex of the sac; on the constantly associated presence of the vesicle with tubes adhering to the apex of the sac*; on the occasional indications of a direct passage between these; and on the changes the vesicle subsequently undergoes.

The appearance of this vesicle is almost always that of a rounded cell containing molecular matter, at first very mobile: very frequently a neck is obvious, which, however it may appear at first sight, always corresponds in direction with the opake line in the centre of the apex of the sac, and which is in my opinion the line of passage followed by the *boyaux*. The margins of this vesicle are almost always such as a simple sac would present; occasionally it has appeared to be lobed, and occasionally I have seen indications of another vesicle. Such appearances as these last I would endeavour to explain by supposing the penetration of two or even more *boyaux*, the application of more than one not being very uncommon.

The occasional appearances of inflection are such as would arise from the relations of a vesicle that has penetrated a grumous, often, as it appears, a bilobed mass, to that mass; and it was to explain those appearances, which are common, that I paid particular attention to the intimate structure of the apex of the sac before fecundation. And I beg distinctly to state that I have seen no appearances that would lead me to consider that the sac itself suffered any considerable or constant inflection before the *boyaux*.

The vesicle has appeared to me generally to remain unchanged until the nucleary aggregation of the molecular matter of the sac has reached to some extent; its free margin I have then found to present traces of internal division, first pointed out by nucleary aggregation, then by the shadowing out of as many cells as there are nuclei; the further changes it undergoes will be subsequently noticed.

In *Osyris* I was not able to detect any inflection or penetration of the sac of the embryo by the *boyau*. This seemed merely to expand upon the sac, occasionally causing indentations on its surface: indeed it appears to me that penetration would in this instance present an unexampled anomaly.

* To this I have only met with one exception, although I have examined some hundreds of sacs. Yet it would seem obvious that the *boyau* might be as liable to break off within the teeth of the apex of the sac as without.

It is probable that the curious form of embryo-sac, so conspicuous in *Santalum* and in *Osyris*, is of general occurrence in the natural family *Santalaceæ*. I find, on referring to notes made in 1836, that a sac resembling that of *Osyris* at its anterior, and that of *Santalum* at its posterior end, would appear to exist in a Santalaceous genus, probably allied to *Sphærocarya**.

On the functions of the anomalous extension backwards I am by no means inclined to advance any opinion. In establishing (or tending to do so) a direct communication between the young seed and the vascular supplies, as they diverge from the apex of the pedicel to their destinations, it may be considered as analogous to the raphe of an ordinary ovulum. In its structure, however, and more especially the direction of its development, it appears to be opposed to the usual form of raphe. It must also, I think, be remembered, that in *Loranthus*, in which the same necessity of communication may be assumed to exist, it does not appear to do so; and that instances are not, perhaps, uncommon of ovula of ordinary form having no vascular or tubular connexion with the vascular supplies. Neither must it be omitted, that in *Santalum*, at least, there would appear to be a want of communication between the ends of the extensions backwards and the vessels derived from the pedicel, and that those of the barren ovula are equally, or nearly so, developed with those of the fertile one.

It would appear that these functions, whatever in reality they may be, do not extend throughout the formation of the seed; for not only does the placenta seem to be torn up to a considerable extent from its original connexions, but the tissue around it becomes altogether broken and dried up.

From the consideration of *Santalum* and *Viscum*, I had been led to adopt the opinion that the embryonary sac was probably the only essential part of an ovulum. This opinion was formed on the apparent inutility of the nucleus of *Santalum*, so far as its later functions were concerned, on the apparent universality of existence of the embryo-sac, and on the structure of the Mergui *Viscum*†. And when I first examined the structure of *Loranthus bicolor*, I

* I would recommend the prolongation of a membranous tube from the base of the ovulum backwards as one test of the affinities of *Santalaceæ*.

† It is with reference to the determination of absolute *essentiality* that precise observations on the origin of the sacs of *Loranthus* and *Viscum* are so necessary. Analogy would lead me to suppose that some extent of nucleary base was indispensable.

was inclined to consider that a reduction of parts similar to that which constitutes in my opinion the second modification of *Viscum*, occurred in *Loranthus*. But the obvious continuation of the tubes or sacs high up the stigmatic canal seemed to present very obvious analogies with what is known of pollen tubes. Besides this, the growth of the great bulk of cellular tissue, constituting the first steps in the development of the embryo, could not be made to agree in direction or situation with the similar growths in any modification of this sac known to me. With the view of determining this point, I endeavoured in many instances to trace the tubes upwards to the stigma, and, if possible, to the pollen grains; but I did not succeed in tracing them more than half-way up the style, nor is this particular species well calculated to promise success from the length of the style.

Although I do not see any absolute theoretical objection to the attachment of an ovulum to any part of the stigmatic canal, the inner surface of which appears to me to have such direct relations with the placentæ; or to its being reduced to a simple membranous sac; yet the analogies were, I thought, in favour of the derivation of these tubes from the pollen grains. And yet, contradictory as it may seem, the arguments on which I founded this opinion were of a negative character, with the exception of that which regards the relation of an ovulum with the stigmatic canal, of which no instance was, I believed, known; for *Osyris* had rendered inapplicable a rule otherwise very general, and so far as I previously knew, perhaps universal, that when an embryonary sac exists, the embryo is developed within it.

I also adverted to the fact of the tubes not appearing to exist before the dehiscence of the anthers, and to their similarity in structure and appearance to *boyaux*. But the first point, otherwise of minor importance, is much weakened by *Viscum*, as detailed by M. Decaisne; and between that form of embryo-sac, which is derived from the extension of a single cell, and pollen tubes many things may be common. Both are membranous and extensible; both are generally the innermost membranes of their respective structure; and the contents of both appear to me to be much the same: and I need only allude to *Santalum* to point out the great similarity that may exist between a pollen tube and an embryo-sac. To these I added, that if they were embryo-sacs, there are grounds for supposing that to each sac there would be an embryo. I therefore inclined to the opinion, that in *Loranthus* there was nothing analogous

to an ovulum, and that the cellular growths constituting the young albumen and young embryo took place from the ends of the pollen tubes themselves.

This view, which appeared in the 'Gardener's Chronicle,' No. 12, March 1841, p. 182, was not corroborated by subsequent observations, made first on *Loranthus globosus*, in which two of the greatest obscuring causes occurring in *Loranthus bicolor* do not exist; the embryo-sacs in the former being confined to the ovarium, and not appearing to be endowed with independent powers of growth. My present opinion regarding *Loranthus*, as exemplified by the two species I have endeavoured to illustrate, is, that its ovula are reduced to the simplest possible form which an ovulum can assume with reference to the present generally received opinions of this organ. They who follow M. Mirbel may imagine a simpler form still; but I believe that his quintine is the embryonary sac, or the fourth envelope of almost, and perhaps all, completely developed ovula. As, however, both M. Schleiden and M. Decaisne appear to consider the reduction as carried on to a minor extent, I shall mention the reasons which have induced me to adopt the opinion above stated.

Of the grounds on which M. Schleiden has based his opinion, that "the point of the nucleus (of *Loranthus*) is lengthened so as to assume the appearance of a style*," I regret I am ignorant, because this botanist has appeared to me, since the publication of his memoir "on the Development of the Organization in Phænogamous Plants," to be one of the greatest authorities on structural points.

With M. Decaisne's observations I am acquainted through the 'Comptes Rendus' of the Academy of Sciences of Paris, No. 6, Fevrier 11, 1839, and through a translation of his paper "on the Development of the Reproductive Organs of the Misletoe" in the 'Annals and Magazine of Natural History,' May 1841.

From not having found any opening in the ovulum, M. Decaisne comes to the conclusion that the ovulum of *Viscum album* is a naked nucleus, reduced to its simplest form,—a sac inclosing the embryo. As, however, M. Decaisne states previously a well-known fact, that an inner closed envelope is of general occurrence among ordinary ovula, it is evident, I think, that a simpler form

* These are, I believe, the words of M. Meyen in one of his Reports on the Progress of Physiological Botany, which I have not now by me.

than such an ovulum as he describes may exist, as appears to me to be pointed out by *Santalum* and *Thesium*. The nucleus of an ovulum is the part first formed: in the direction of its growth it obeys those laws that regulate all extensions of the axis, its apex being formed first, and once formed, always continuing to be the apex, and it is always as compound in its commencement as any direct extension of the axis is at its commencement. None of these conditions are fulfilled by the sacs in question; and in *Viscum album* the direction of growth appears to be quite reversed.

There are also two other circumstances, which, I think, are corroborative of my opinion, namely, the development of the albumen in the interior of the sacs of *Viscum* and *L. globosus*, and the absence of a sac surrounding the embryo; circumstances which, taken together, are, so far as I know, contrary to every analogy.

Considering, then, their late development, their structure, which is that of almost all albuminigerous embryo-sacs, and which is so unlike that of a nucleus, their similarity in the same respect to the embryonary sac of *Santalum*, *Thesium*, *Osyris**, &c., I have little doubt but that they are the analogues of ordinary embryo-sacs, although I am by no means certain, from not having seized on their first development, that the anomalies may not be so great as I have conjectured: for to each sac there may be a nucleary base, or indeed a common one; for I see no reason why exsertion should not occur in nuclei with several embryo-sacs as in those with only one.

With the exception of the structure of the sacs, and their perforation longitudinally by the pollen tubes, the sacs of the two species have not much in common; for while in *Loranthus globosus* they have not very extraordinary limits, in *L. bicolor* they are found a long way up the stigmatic canal; and while in the former species the albumen has its usual relations only partially interrupted, in *L. bicolor* these appear almost, if not quite, entirely destroyed; and what is very remarkable, the sacs have to a certain extent proper powers of productive growth. Cellular subdivisions likewise make their appearance in both species *above the albumen*; and consequently in *L. bicolor*, in the sac itself. I am unable to state whether these really enter into the composition of

* The sacs of *Viscum album* appear to disagree remarkably in not being simple extensions of a simple cell.

the albumen: if they do, it would appear to be, at least in *L. bicolor*, to an inconsiderable extent.

The relations between the pollen tubes and these sacs in both species appear to me very singular. In the first place, the point of entrance is in *L. bicolor* not always single or in the centre; in the second, the tubes have appeared almost invariably to be two; in the third they do not undergo the ordinary changes until they appear to have reached or passed beyond the posterior ends of the sacs. On these singular points my limited experience can bring nothing to bear.

4. *Origin of the Embryo.*

The first process in the development of the seed, subsequently to the penetration or application of the *boyau* to the embryo-sac, would in *Santalum*, *Osyris*, *Loranthus* and *Viscum* appear to consist of the formation of cellular tissue. This may be applied, I believe, to most if not to all instances. This cellular tissue appears to have two different origins; one, and this is the earliest in development, being perhaps referable to the embryo-sac, while the other appears directly referable to the anterior ends of the pollen tubes. The amount of both these tissues may vary considerably; and it may probably be found that whenever the first is developed in any quantity, the subsequent presence, or rather, perhaps, permanence, of albumen is determined*: the second may be limited to one or to a few cells, forming the funicle or "suspensor" of the embryonic mass; or it may be developed to a great extent, as in *Loranthus globosus* and certain Gymnospermous plants; or, as *Viscum* would seem to intimate, the pollinic vesicle or anterior end of the pollen tube may develope within its interior the proper tissues of the embryo.

In no instance, perhaps, where the embryo is developed from the ends of the pollen tubes, does it become developed so immediately that no cells intervene between it and the end of the pollen tube; this is particularly evident during the earlier stages of development.

That part of the embryo in which the condensed tissues occur, and which, from its appearance and frequent tendency to constriction round its base, I

* *Santalum* and *Loranthus*, but especially *L. bicolor*, seem to me to indicate that the albumen is probably derived from the embryo-sac, which would thus appear to be, at least in some measure, a potential organ.

at first suspected was the only part of the embryo (the rest being then funiculus), corresponds, I think, in situation with the *collet*; it is very evidently not the point of the radicle, for this will subsequently be found so close to the vesicle as to authorize me in assuming that the greater part of the soft cellular tissues becomes the body of the root.

Up to the appearance of the very original memoir of M. Schleiden "on the Development of the Organization in Phænogamous Plants," with which I am acquainted through a translation in the 'London and Edinburgh Philosophical Magazine' for 1838, our knowledge of the origin of the embryo was by no means definite. My own acquaintance with the subject did not extend beyond the penetration of the nucleus by the pollen tube or tubes to a considerable depth in many instances. So far as I can understand the translation, it would appear that the growth of the embryo must take place from the inflected end of the embryo-sac. But this certainly does not agree with a subsequent passage, which I have elsewhere quoted, relative to the entrance of the pollen tube into the sac of the embryo, and the gradual conversion of its end directly into the embryo. Nor does it agree with the plates, which correspond with the passage just referred to and with my observations on *Santalum*, and agree well with those on *Loranthus*.

If M. Schleiden is of opinion that in general the *boyau* penetrates into the embryonary sac, and that the embryo is derived from its intruded extremity, as indeed he has delineated it, *Santalum* and *Loranthus* become strong corroborations of so grand a doctrine, and *Osyris* an exception confirmative of the rule.

But none of my observations have tended to confirm his idea of the inflection of the embryo-sac before the pollen tube; and it appears to me sufficiently obvious, that if such were the case, the cylindrical bag constituting the "*embryo in its first stage of development*" would consist of three membranes or layers: viz. the first or outer, of the ordinary and uninflected membrane of the sac; the second, of its inflected portion; the third, of that of the pollen tube itself. It is also worthy of attention that M. Schleiden makes no mention of the ultimate fate of the inflected portion, which in his illustrations is only represented as partial, and precisely such as might be expected to occur during the *gradual*?? intrusion of a membranous tube into a membranous or membrano-cellular sac.

M. Schleiden assumes the applicability of his conclusions, drawn from direct observation in several plants, to all others in which direct observation is more difficult, on three distinct grounds; the first of which, regarding the diameter of the tube outside the sac and just within it, is, I cannot but think, of very minor importance, neither does it present itself in *Santalum*; the second, which would confine certain peculiar contents to the pollen tube, appears to me contradicted by *Santalum* and *Loranthus*; and the third, which positively refers plurality of embryos to a plurality of pollen tubes, is contradicted in a most marked manner by *Loranthus*.

I am unacquainted with any other observations on this most interesting point, except those of M. Mirbel, which were, in France, I have reason to believe, considered to carry a signal refutation of the views of M. Schleiden, but which certainly have not convinced me; and I cannot help imbibing the belief that the primordial utricle of M. Mirbel and M. Spach is the sac of the embryo, which no doubt often, and perhaps generally, exists before fecundation.

M. Mirbel has thus summed up the conclusions arrived at by M. Schleiden regarding the relations of the *boyau* and the sac of the embryo; and I quote it to show, that he has put on it a construction similar to that which I have previously ventured to do:—"Quand la cavité ovoide s'est accrue et en même temps le sac embryonnaire qui la tapisse, le boyau issu des grains du pollen pénètre jusqu'au sommet du nucelle, pousse en avant la paroi du sac embryonnaire, qui çède à sa pression, et forme un cæcum dans lequel il loge son extrémité antérieure.

"La partie du boyau pollinique logée dans le cæcum se renfle en massue et produit, dans sa cavité, un tissu utriculaire qui la remplit et se moule sur elle; tandis que la partie postérieure de ce même boyau reste en dehors sous sa forme primitive de tube membraneux. Cette partie ne tardera pas à disparaître; l'autre, métamorphosée en embryon, commencera une nouvelle génération*."

To that which regards the inflection of the sac of the embryo before the pollen tube I at least attach considerable importance, because it appears to me to weaken if possible the great merit of M. Schleiden's observations, and to

* Comptes Rendus, No. 12, March 25, 1839.

give my own a better claim perhaps to notice. With the exception of this, and such part of my own observations as would refer the embryo, for the greater part, or perhaps entirely, to a growth *from* the ends of the pollen tubes, except in *Viscum*, I cannot but hope that these present observations will be considered to be striking corroborations of the general views of M. Schleiden. Of M. Wydler's observations I have no knowledge but that very lately derived from an able summary by Dr. Giraud of the recent doctrines of vegetable embryology in the 'Annals of Natural History,' No. 31, June 1840, and which therein only go so far as to establish the points of non-inflection of the sac, and of the entrance of the pollen tubes into it. On the general subject of the vegetable ovulum I hope to enter into detail as soon as the proper opportunities offer, not so much in the hope of producing anything new on a subject on which Mr. R. Brown, and MM. Schleiden, Mirbel and Brongniart have been engaged, but to extend the application of the facts established by them to plants out of the reach of European *savans*.

The growth of a tissue from the ends of the pollen tubes, from which tissue the embryo of *Loranthus* is directly formed, appears to me to open to view glimpses of the most beautiful analogies.

In the sporula, so called, of the more developed Acotyledonous plants, we have organs consisting of two envelopes; the inner of which contains granular matter, has remarkable powers of growth, and, so far as function is concerned, appears to be alone essential. The proper stimulus calls this membrane into growth, and from the apex of its extension cells are developed; from these others again are produced; and from the centre of the mass thus formed, originates at a certain period the growth of the true axis.

Similar phænomena take place in the formation of the seed of Phænogamous plants, with this difference, that the albumen, unlike perhaps the *thallus** of the Acotyledonous plant, is not a direct growth from the pollen tube. Such other differences as appear to exist are of minor importance; they consist in the different nature of the stimulus calling forth the extension of the inner membrane, in the condensation of the growths forming the seed, which may be reasonably inferred to arise from the confined situation in which they

* Am I right in the use of the term thallus? by which I mean, the confervoid mass first formed in the germination of Acotyledonous plants, such, for instance, as *Equisetum*.

occur, and in the cells composing them containing fecula, not green globules, also apparently a consequence of the confinement alluded to. The functions of the intermediate growths are in both precisely the same, viz. that of nourishing the young axis until it is sufficiently matured to enable it to maintain an independent existence.

The germination of such Acotyledonous plants appears therefore to me to be analogous to the development of the seed of Cotyledonous plants*, and the perfect state of the lower is analogous to the imperfect state of the higher organization. And to a similar observance of the phases of development I am tempted to attribute the prevalence of albumen in Monocotyledonous plants, although this is apparently strongly contradicted by the occurrence of the most exalbuminous and perfect Monocotyledonous embryos in the least organized plants of the class, and perhaps equally so by its prevalence in the monopetalous division of Dicotyledons.

The analogy between the spore and the grain of pollen has long been remarked; and its extended application to the processes, constituting germination in the one instance, and the formation of the seed in the other, was given by Mr. Valentine in 1833†. I think I am correct in naming it analogy rather than affinity, from considerations derived both from development and functional powers. For the spore of these particular or more developed Acotyledons is not produced by a comparatively simple process as the pollen of Cotyledonous plants is, but is the result of a process as complicated, if not more so, than the development of the seed, and, in addition, presents in its first stages very curious similarities with the development of a true ovulum. Both agree in being set in action by the agency of a comparatively simple structure; but the early complication of the process in the higher Acotyledonous plants would at once lead me to suspect that the organs alluded to are not strictly similar; for the earlier we proceed in our investigations, the more marked should be the resemblance, and the more simple both structure and function. The powers of growth in the two are remarkably contrasted, and

* The confervoid growths of Acotyledones, which I thus speculate to be analogous to the albumen of Cotyledones, may be, for aught I know, considered by others to be analogous to their cotyledons; but their irregularity of growth appears to me an objection to this view.

† Linn. Trans. vol. xvii. p. 480, last parag.

will be still more so, if the albumen be ultimately found to be derived from the female.

M. Schleiden, on the contrary, is of opinion, that between the spore and the embryo there is an affinity amounting to fundamental unity; and Mr. Valentine not only holds the same opinion, but, overlooking the obvious difficulties to which M. Schleiden has adverted as presented by some of the higher Cryptogamic families, denies to these plants *entirely* a provision similar to that of the pistillum of Phanerogams*.

In the present state of our knowledge, I should be extremely unwilling to

* The question of the sexuality of Acotyledonous plants is so intimately connected with the subject of vegetable embryology, that I trust I shall be pardoned for hazarding a few observations derived from personal experience: it is a question which the hypothesis of M. Schleiden necessitates him, as it were, to disbelieve.

The more developed Acotyledonous plants, which I take to be *Filices, Lycopodineæ, Isoetes, Marsilea, Salvinia, Azolla, Hepaticæ* and *Musci*, appear to me to present two very distinct types of organization, at least as regards the female organ. In one type there is an evident pistillum containing an ovulum, and this appears to be generally connected with limited development of the organs of vegetation. In the other there is no evident pistillum, nor any palpable point on which analogy would indicate that the male influence would be exerted. That type is also remarkable for the development of the organs of vegetation.

In *Musci*, the evidence of the mutual action of the sexes appears to me very satisfactory; the usual discoloration of the stigma and canal of the style is distinctly observable, and is followed by changes, confined, however, to change of situation, affecting the cell pre-existing in the cavity of the ovarium, and which is analogous to a Phænogamous ovulum. In *Hepaticæ*, particularly the vaginulate species, the circumstances would appear to be the same: and in the evaginulate ones, and perhaps also in *Riccia*, still nearer approaches are made by the changes which the pre-existing cell undergoes to the ovulum of Phænogamous plants.

In the *Azolla* I have examined, which is the only other plant which appears to me pistilligerous, for I have no knowledge of the development of *Salvinia*, the pistilla in each involucre are two, and both present the appearance so generally characteristic of fertilization. The changes subsequent to this are however very different, giving rise in one pistillum to the supposed male, in the other, to a series of sporules derived from the characteristic dividing process.

On *Lycopodineæ* I have no observations, and on *Filices* merely a few surmises to offer. I believe that every species will be found to present a male apparatus, which, I think, was first pointed out by the great Hedwig, and subsequently by M. Link. I have lately alluded to it without having any previous knowledge of the labours of the two above-mentioned botanists. The fertilization of Ferns I believe to be interpreted by *Anthoceros*, provided my observations on that genus be found to be correct. The only difficulty exists in the anthers not appearing, in some cases at least, to dehisce; but I beseech botanists not to cast away the opinion of the very important nature of these bodies on a solitary objection; they will remember that until very lately an absorptive process was generally adopted to

adopt the curious conclusions of M. Schleiden regarding the ordinary opinions of the distinction of sexes. Neither do I conceive that those opinions can be legitimately derived, until, *at least*, the total absence of an ovulum shall have been ascertained. The female organ is still the organ of gestation, if we assign the very lowest degree of value to it, which even the instance of *Viscum album*, as explained by M. Decaisne, does not at present authorize us to do. And this would still have been the case, even though my first version of the phænomena of *Loranthus bicolor* had proved to be correct. Neither am I at all willing to imagine that the analogies between the animal and vegetable

explain the fecundation of *Asclepiadeæ* and *Orchideæ*, and even adhered to, when a beautiful train of reasoning and observation had reconciled them, in all the essential points, to the ordinary plan[1].

With regard to *Marsilea*, I have to remark that the observations of M. Fahre, as given by M. Dunal (Ann. Sc. Nat., N. S., t. vii. p, 221), scarcely agree in one particular with some observations on a *Marsilea*, I believe *M. quadrifolia*, made by myself at Bamo on the Irrawaddi in 1837. In the species I then examined I found the organs to be of two distinct kinds, attached to the veins of the involucre. Of these two kinds, one only is subsequently subjected to the usual ternary or quaternary division, from which result bodies altogether similar to the acknowledged spore of other Acotyledonous families. The other body has no analogy in my opinion to the acotyledonous form of anther. In *M. Fabrei*, however, the females have been represented as having curious analogical resemblances to the Phænogamic pistillum; and what is, perhaps, more extraordinary, the anthers are said to be simple sacs containing granules and molecules, and apparently are similar to the pollen of certain *Naïades*, *Balanophoreæ*, *Rafflesiaceæ*, &c.

In *Isoetes* the males of authors are nothing but modifications of the spore; and in *I. capsularis*, Roxb., they seem to be merely temporary modifications. They have, in fact, so precisely a common development, that it is scarcely allowable to allot to them the performance of such opposite functions as those usually attributed to them. The true male may, perhaps, be found in the cordiform, fleshy lamina above the receptacle of the spores, from which it is separated by a lamina perhaps analogous to the indusium.

The transition between the two types exists in *Anthoceros*, which in the development of its anthers

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[1] Nothing has been more detrimental than the writings of those "mere theoretical botanists," who have advocated asexuality, as if it were the usual plan of Nature, and who have indignantly remonstrated against those who have attempted to reconcile glaring inconsistencies. What has been the consequence? Instances of each of the higher Acotyledonous orders exist within the limits of Europe, but any precise and comprehensive knowledge of them can scarcely be said to be within the limits of its natural science. With the exception of Mosses, *Hepaticæ* and *Pilulariæ*, nothing is absolutely known of the real structure of these particular plants. And nothing can be more mischievous than the adoption of such terms regarding these plants as *Antheridia* and *Sporangium*; they have answered their purpose of checking inquiry, by making believe that they are absolute or non-analogous organs.

kingdoms, so far as regards composition, growth and nature of the axis, and reproduction, will be found so inconstant, indistinct and uninstructive, as to merit the appellation of being "lame*," or to be considered as causes of embarrassment.

It follows from the consideration of *Santalum* and *Viscum*, and still more so from that of *Osyris* and *Loranthus*, that the expression of the law regulating the relation of the radicle of the embryo to the parts of the seed, and more especially to the apex of the nucleus, must undergo considerable modification. For in *Santalum* it is evident that the radicle points from, and not towards the apex of the nucleus; and this organ is, I think, at any rate not practically appreciable in *Viscum*. *Osyris* shows that the expression of the law cannot

and habits has much in common with the pistilligerous type. In this genus the male influence is first exerted on the surface of the frond, and thence is extended through the upper parenchyma to that part of the substance of the frond from which the reproductive organ is to originate. So far as I know, nothing like a pistillum appears to exist: and though there is a calyptra, it has nothing, except situation, in common with the calyptra of *Musci* and *Hepaticæ*, being only that portion of the parenchyma between the surface of the frond and the spot whence the young reproductive organ has originated [1].

I take it to be a valuable example, inasmuch as it shows, if my explanation be correct, that the male may not only act successfully without a pistillum or any similar co-existing body, but that it may act mediately. Consequently, Ferns are easily, and I think fairly, explainable, provided the glandular hairs are allowed to be the males. And in what do they differ from the anthers of certain *Musci* and *Hepaticæ*, or from the anthers of Phænogamous plants, when they are cellular, undivided bodies, containing grumous molecular matter? In regard to points like these, most botanists have, like some zoologists, pitched upon one standard of organization, and that at the wrong end of the scale. But those who look for a smaller degree of complication in low organizations, or for a greater degree of reduction to the elementary substances, will, I think, not only admit that the anthers of all the above families, so far as they have been well observed, have a marked correspondence with, but that they are also analogous to, very young anthers of Phanerogamous plants. I might ask, what have they in common with *gemmæ*? is the structure of a *gemma* compatible with a cellular sac containing a grumous matter? is the function of a *gemma* more compatible with such a sac, often inclosed in a cavity in the frond, from which it does not escape, and in which they are, *functi officiis*, to be found in the shape of withered empty sacs?

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[1] I advance this with some hesitation, as *Anthoceros* is, I believe, generally considered to be calyptrate. My own observations, which were only casual, were made in Assam early in 1836, and since then I have had no opportunity of revising them. From what I then noted, I think few plants would better repay the minutest investigation.

* Vide Schleiden's 'Memoir,' *op. cit.* p. 245, middle parag.

be made to refer even to the apex of the embryonary sac: and in *Loranthus*, if my explanation be correct, it is at once obvious that the radicle can have no primary relations to the ovulum, and, indeed, no secondary ones to those parts of the seed from which have been derived the expressions regarding its direction. To include all these anomalies, the wording of the law must perhaps be made to refer to the pollen tube.

I now pass to a recapitulation or summary of my ideas of the structure of *Santalum*, *Osyris*, *Loranthus* and *Viscum*.

In *Santalum* the ovulum consists of a nucleus and an embryonary sac, prolonged beyond both the apex and base of the nucleus: the albumen and embryo are developed in the part above the septum, the part below and the nucleus remaining unchanged. The embryo is developed from the pollinic vesicle. The seed has no actual proper covering, and no other theoretical covering than the incorporated upper separable part of the embryo-sac.

In *Osyris* the ovulum is reduced to a nucleus and an embryonary sac, which is prolonged in the same directions as *Santalum*, but not to such a degree beyond the apex of the nucleus. The seed is formed outside the embryo-sac, and is absolutely without proper tegument, or whatever covering it may have did not enter into the composition of the ovulum. The embryo appears to be developed at some distance from the anterior end of the pollen tube.

In *Viscum* the modifications appear to me to be two: in the one, an evident cavity exists in the ovarium; and the ovulum appears to be reduced to an embryonary sac hanging from one side of the base of a nipple-shaped or conical placenta; in the other, the ovulum is reduced to an embryonary sac, but this is erect, and has no such obviously distinct point of origin as in the first. In both, the albumen has no other proper covering than the incorporated embryonary sac; and, at least in the last, the embryo appears to be a direct transformation of the pollinic vesicle.

In *Loranthus*, each ovulum appears to be reduced to an embryonary sac; the albumen is developed either partly within the sac, or entirely, or almost entirely, without it. The embryo is a growth from the ends of the continuations of the pollen tubes *outside the anterior ends of the embryo-sacs*; and is, in one modification, exemplified by *L. globosus*, up to a certain period exterior even to the albumen. In *L. bicolor* the albumen has no proper tegument;

in *L. globosus* it may be supposed to have a partial one in the incorporated albuminous part of the embryo-sac.

The gradation of structure appears to me to be tolerably complete. One modification of *Viscum*, in my opinion, tends to show, that in *Santalum* the first steps towards the disappearance of the usual nucleus take place; *Osyris* seems to me to indicate that a similar tendency may affect the embryonary sac; and *Santalum* appears to me to allude to a reduction in the embryo-sac to the form of that of *Osyris*. Nor is this all: *Osyris* has its albumen and embryo developed outside that end of the sac to which the pollen tubes are applied; *Loranthus bicolor* has the same developed outside the opposite end of the sac; and the partial development of the albumen in the embryo-sac of *Loranthus globosus* may perhaps be a passage to its development outside that sac in *L. bicolor*.

The novel points of structure and development indicated in this paper are, so far as I know, the possibility of the separation of a continuous membranous embryo-sac into two distinct parts, of which the lower remains unchanged, though it would almost appear from *Osyris* to be the most permanent; the presence of the embryo-sac not being necessarily connected with its forming one of the constituent parts of the young or of the mature seed; the longitudinal percursion of the embryo-sac by the pollen tubes; the formation of the albumen, either only partially within the embryo-sac, or almost entirely, if not quite so, *without* it; the confluence of the albumina of several sacs into one albumen; the growth of the embryonic tissues from the continuations of the pollen tubes outside the embryo-sac; the possibility of one embryo resulting from a combination of several pollen tubes, and of its becoming interior to the albumen, although it may have been for some time entirely exterior to it. I make no mention of the posterior prolongations of the sacs, in doubt of the true nature or origin of the so-called chalazal apparatus of *Thesium*; or of the growth of the embryonic tissues from the ends of the pollen tubes, in doubt of my having misunderstood the observations of M. Schleiden, and in ignorance of those of M. Wydler.

To the observations on *Santalum* it may be objected, that the continuity of the vesicle within the apex of the embryo-sac with the tube adhering to its apex, and of the tube with the interior membrane of the pollen grain.

has not been shown; that the identity of the vesicle with the uppermost less cellular part of the whole mass of the embryo has not been ascertained; and further, that the frequent appearance of this as having on separation an entire margin, is an objection to its having been derived from the pollen tube.

To put beyond doubt these objections, and many others that will of course *generally* suggest themselves, would exceed my ability. I am satisfied if the results are considered to be not altogether unreasonably arrived at, and if they are found to agree with the aggregate results of others' experience.

In no instance has the structural investigation of any particular plant been pushed so far as to leave nothing to be desired by the observer, or to be observed by others. Actual observation of all the minuter points of structure is scarcely to be expected in any plant, for the advantages it may present in some respects will probably be counterbalanced by disadvantages affecting others; so that our knowledge of structure is more derived from numerous incomplete, than from a few complete observations.

Although few plants can be supposed to present such facilities for observing the circumstances attending the establishment of direct relations between the embryonary sac and the end of the pollen tube, the opacity and, so to say, the callosity of the apex of that sac present positive disadvantages. And the subsequent cellularity of the sac reduces again the facility of determining the identity of the original vesicle, and the upper less cellular parts of the embryonic mass.

From such experience as I have been able to collect, I have derived a conviction that, whenever filaments, *such as pollen tubes are known to be*, are found in the canal of the style *only after* obvious action of the pollen upon the stigmatic surface, and that these are traceable downwards directly into the ovula, it is legitimately assumable that those filaments are pollen tubes; and I proceed on this assumption to observe the consequences, as if I had actually ascertained the continuity of the filament with the inner membrane of the pollen grain.

With regard to the identity of the vesicle with the uppermost less cellular part of the mass of the embryo, I believe that few persons would have examined a numerous series of fecundated ovula without coming to the conclusion which I have ventured to advance; it occupies the situation that the vesicle

did, and the circumstances I have detailed regarding it are not, I think, inconsonant with analogy.

The objection deducible from some parts appearing, when separated, to present an entire edge, may be waived on the score of the minuteness of the observation which would relate to a cicatrix or scar of separation of an undilated part of the pollen tube. Besides, I would be by no means disposed to deny that a plant may have the power of closing up such a solution of continuity, as must be admitted to have occurred, if my opinion of the origin of this vesicle be correct.

So far as the other instances which I have endeavoured to illustrate are concerned, more exact inquiries are very necessary, particularly as regards the origin of the albumen in *Osyris* and the relations of its young embryo to the pollen tubes. As regards *Loranthus*, further observations are required on the state of the pollen tubes intermediately between their penetration into the sac and continuation beyond it: on the state of the embryo-sacs at the time the pollen tubes are continued beyond them: on the degree to which the embryo-sacs of *L. bicolor* may develope albumen in their interior, and those of *L. globosus* above that part of the sac in which the albumen first makes its appearance. Lastly, as regards *Viscum*, especial inquiry is requisite concerning the origin of the ovulum—this holds good equally with those of *Loranthus*—and the direct conversion of the pollinic vesicle into the embryo.

The materials for all these, excepting *Santalum* itself, perhaps, exist in the immediate neighbourhood of Malacca.

Malacca, March 28, 1842.

EXPLANATION OF THE PLATES.

[The figures given in the five plates accompanying Mr. Griffith's Memoir have been selected from a very extensive series of drawings forwarded by him from Malacca, as those which appeared best calculated to illustrate the structure of the plants examined, and the views entertained by the author regarding them.]

In the following explanation of the plates I have to observe that no measurements have been given, because I found considerable variety in the state of the fruit, belonging, if size only were consulted, to one period. I have endeavoured to represent the development throughout, so as to give an intelligible idea of the phænomena with which it is accompanied. The dotted lines visible in several of the sketches exhibit what I conccive to be the situation of parts removed from direct vision, and supplied by actual dissection; so that these sketches approach partly to the nature of *plans*. As such I submit them with great deference; for however easy a tolerably accurate delineation of what is under the eye may be, the sources of error are much increased when minute internal parts are filled up from the ideas of their relative situation derived from dissection.

Tab. XVII.

Santalum album.

Fig. 1. Apex of an embryonary sac, of its perfect form; showing the apex to be apparently divided, with fissures between the divisions, which look (in this one instance) as if they originated from the membrane of the sac itself. The grumous nature and division of the contents of the upper part of the sac, and the grumo-molecular nature of that below, are distinctly seen.

Fig. 2. Apex of another sac, intended to show (at *a*, *a*, *a*) the limits of the originally simple sac.

Fig. 3. Placenta halved irregularly, from a fully-expanded flower. Generally there is no difference in length between the posterior extensions at this period.

Fig. 4. Apex of an embryonary sac. The tube, near its broken edge, looks as if incrusted with patches of grumous matter; these are the aggregations of the grumous granular matter, and form the prelude to the subsequent cellularity.

Fig. 5. Bulb of a more developed sac. *a*. The septum, which is invariably formed both in barren and fertilized sacs. *b*. Indications of another cell or septum of excessive tenuity.

Fig. 6. Apex of a sac, seen with an object-glass of $\frac{1}{4}$ of an inch focal distance. One of the clearest instances of continuity of vesicle and pollen tube.

Fig. 7. Ovulum, a little after fecundation. The hemispherical part of the bulb is now cellular; nucleary aggregation is distinct at both ends of the tubular portion. The vesicle in this instance was empty. The place of future separation seen at *a*, *a*.

Fig. 8. Placenta, with two fertilized ovula, one a good deal less advanced than the other. The course of the posterior extensions is traced out.

Fig. 9. Whole of the embryonary sac above the bulb. The cellularity of the vesicle is commencing by the usual nucleary aggregation, and its lower part appears as if cut off from the upper. This is, I think, the usual appearance. The pollen tube is still seen in adhesion.

Fig. 10. Apex of an ovulum, or young seed, more advanced. *a.* Vesicle. *b.* Lax embryonic tissue. *c.* Condensed apex of ditto.

Fig. 11. Embryo of the same detached. The upper portion of the vesicle is undivided; this is almost always the case. The letters have the same references as in fig. 10.

Fig. 12. Longitudinal section of young fruit.

Fig. 13. The entire embryonary sac, of this period, dissected from its surrounding tissues, with the exception of the apex of the nucleus.

TAB. XVIII.

Osyris Nepalensis.

Fig. 1. A longitudinal section of the flower, before expansion. *a.* The part which may be supposed to be derived from the adhering integuments of the flower. *b.* The part which I suppose to correspond to the ovarium. *c.* The placenta. *d, d.* Two ovula. *e.* The stigmata.

Fig. 2. The placenta of the same, detached. The ovulum to the right is somewhat displaced.

Fig. 3. Ovulum, during the expansion of the flower. *a.* Nucleus. *b.* Protruded mammilla of embryonary sac. *c, c.* Included portion of ditto. It does not appear to be prolonged downwards.

Fig. 4. Placenta, after impregnation, but before any considerable sphacelation of stigmata. One of the pollen tubes is accidentally ruptured; the other is seen in contact with the protruded apex of the embryonary sac. The dotted line *a, a, a, a,* is intended to show the course of the embryonary sac for some distance beyond the base of the placenta.

Fig. 5. Upper half of one of the ovula, intended to show the relation between the pollen tube and the apex of the embryonary sac. *a, a.* Apex of nucleus. *b.* Protruded end of embryonary sac.

Fig. 6. Placenta, about the period of the fall of the perianthium, detached.

Fig. 7. Ovulum from the same. *a.* Nucleus. *b.* Cellular growth on the protruded apex of the sac; to it a short filament is seen adhering, and in it are seen angular grumous bodies of considerable size. *c.* Part of the embryonary sac.

Fig. 8. A similar ovulum. The dotted line indicates the course of the embryonary sac.

Fig. 9. The apex of an embryonary sac and the cellular growth, from an ovulum of the same period, under pressure. It now appears as if the cells were confined to the margins of the tube. The embryonary sac is separable from the cells even at this stage. The cells are crowded with molecular matter, as is the case in all new cellular growths with which I am familiar.

Fig. 10. Portion of the placenta of a young fruit, with ovulum and young seed. The dotted line represents the course of the embryonary sac.

Fig. 11. Embryo.

Fig. 12. Longitudinal section of a fruit considerably advanced. *a.* Tegumentary tissue. *b.* Circumference of ovarium, now commencing to be indurated. *c.* Loose inner tissue, most dislocated round the seed and placenta. *d.* Communicating canal, still visible. *e.* Placenta and its stalk. *f.* Cellular mass, in which albumen is now deposited. *g.* Embryo.

Tab. XIX.

Loranthus globosus.

Fig. 1. Longitudinal section of an ovarium, $1\frac{1}{4}$ line long. The central tissue of the ovarium, which is (or ought to be) more transparent than the rest, is seen to be occupied by three sacs, the course of which is pointed out (especially in the upper $\frac{2}{3}$rds) by a profusion of granules. The sacs at this period are scarcely separable, nor is their membrane at all distinct: along their lines iodine causes a strong tinge of violet. The sacs extend up into the epigynous disc; some at this period even reaching pretty closely to the base of the style. The dense coniform base of the central tissue, which subsequently effects such changes in the situation of the embryo, now exists.

Fig. 2. Upper end of an embryonary sac, soon after the fall of the perianthium. Owing to the presence of grumous bodies in the apices of the sacs, I never traced the absolute continuity of the inclosed filaments with those projecting from their apices.

Fig. 3. Lower half of an embryonary sac at rather a later period. The limits of the sac are always difficult to ascertain, as there appears to be a tissue formed from their ends. In this instance the limit of the sac is perhaps at *a*, and that of the tissue subsequently formed at *b*. The more condensed tissues of the embryo have made their appearance at *c*.

Fig. 4. From a later period. Three sacs are seen, dissected out of the ovarium: that on the right hand has not been fertilized, and *remains unchanged*; within the others, one of which is broken, albumen is seen to be developed at *a*, *a*; and the albumina

are shown to be percursed by the pollen tubes. These passing out from the albumen at *b, b*, inclosed, as it were, in a cellular case, become confluent at *c*, and then form the funicle of the embryonic tissue, *d*. The green hook visible above this shows, I think, a tendency to the formation of a second embryo.

Fig. 5. A mass of albumen and embryo removed out of the ovarium of a young fruit $2\frac{1}{2}$ lines in length. The embryo is seen to project beyond the lower edge of the albumen.

Fig. 6. Longitudinal bisection of a young fruit, rather more advanced. The mass of albumen is seen to be hollow, the cavity being occupied by the embryo and its twisted funicle, the point of attachment of which to the embryo is shown at *a, a*. The dense obconical base at this period is nearly inclosed in the albumen (although this is not represented), and it does not now separate with the embryo, as it did previously.

Fig. 7. Represents an occasional occurrence of two young albumina remaining distinct to a tolerably late period.

TAB. XX.

Loranthus bicolor.

Fig. 1. Longitudinal section of the base of a bud $1\frac{3}{4}$ line long. *a, a*. Calyculus. *b, b*. Sepals. *c*. Cavity of the pistillum. *d*. Elevated fundus of the cavity. *e*. Dense sublunulate spot of tissue. *f, f*. Vascular supplies of perianthium and stamina.

Fig. 2. Longitudinal section of the base of a bud 12 lines long. *a, a*. Calyculus. *b, b*. Sepals. *c*. Cavity of the pistillum. *d*. Elevated fundus seen through the brownish tissue of base of ovarium. *e*. Dense sublunulate spot. *f, f*. Vascular supplies of perianthium and stamina.

Fig. 3. Longitudinal section of ovarium of a flower before expansion, but fully formed. *a*. Calyculus. *b*. Sepals. *c*. Centre of ovarium, now of brownish subamorphous tissue, occupied by four embryonary sacs, three of which are continued up the stigmatic canal (it is the brownish tissue which obscures so much the original elevated fundus or nipple). *d*. Dense lunulate spot. *e, e*. Vascular supplies.

Fig. 4. Lower part of embryonary sac of the same; the dilated part is that contained in the ovarium;—$\frac{1}{225}$ measured.

Fig. 5. Head and upper part of an embryonary sac, from the same period, found $1\frac{2}{10}$ inch up the stigmatic canal; it is crowded with grumous matter;—$\frac{1}{250}$ measured.

Fig. 6. Head of an embryonary sac, after fecundation. It contains two inner bags prolonged below into tubes, and yet only one pollen tube is seen to penetrate.

Fig. 7. Part of an ovarium from a flower shortly after the fall of the perianthium. The style is fuscous throughout the lower half, and tinged with red throughout the upper half. In the specimen dissected there were three sacs (only two, however, are

represented in the drawing), in none of which were inner tubes detected: two of these were cellular at their lower free ends, and one remained in its original state.

Fig. 8. An ovulum at a somewhat later period, partly dissected away from the closely-adhering tissue of the interior of the ovarium. The lower parts of two sacs are shown, of which one is torn up, disclosing the two inner tubes.

Fig. 9. The young seed, dissected out. In this instance, of three sacs two retained their original appearance, and did not even assist in the formation of the cellular mass, the subsequent albumen. This, as well as the embryo, which is of some size, belongs to the central sac, in which pollen tubes are visible. The young albumen, allowance being made for its having been dissected partly so as to expose the embryo, appears of somewhat confervoid growth.

Fig. 10. Portion of a seed, more advanced, with the albumen cut away except at the base. At this period the base of the albumen (the original cellular mass in which the young embryo was formed) is of a laxer nature than the rest, from which it is sufficiently distinct.

Tab. XXI.

Loranthus bicolor.

Fig. 1. The second cellular sac from the ovarium figured in Tab. XX. fig. 7, magnified about 200 times.

Fig. 2. A fertilized sac of another ovarium, about the same period. *a*. Its constricted upper end, where it becomes engaged in the canal of the style. *b*. What I take to be the situation of the original free end of the sac, beyond which the inner tubes extend very little. In this, as in most other instances examined, the articulations of the inner tubes become shorter and more frequent from the commencement of the cellularity of the sac.

Fig. 3. A young seed, somewhat more advanced than that figured in Tab. XX. fig. 9. Of the three sacs represented as assisting in its composition, two have inner tubes, the growths from which pass through the cellular body and reach its lower surface, which is obscured by adhering grumous tissue. The third sac, although cellularly subdivided to a considerable extent, remained unfertilized.

Fig. 4. Young seed more advanced than that figured in Tab. XX. fig. 9, with the albumen laid open to expose the embryo.

Viscum.

Fig. 5. Longitudinal section of a female flower before expansion. *a*. Outer or bracteal layer. *b*. Point of insertion of perianthium. *c*. Lageniform central tissue. *d*. Opake

submammillate base, from which the sac always seems to arise. *e.* Embryonary sac.

Fig. 6. Embryonary sac before fecundation from ovary before expansion of perianthium, surrounded at its attenuate base by nucellar cellular tissue, from one of the cells of which it may be supposed to have originated.

Fig. 7. Embryonary sac, some time after the fall of the perianthium, with considerable development in the cellularity of the sac, each of the cells of which are very large, and each for the most part occupied by single grumous masses. At *a*, the perforation of the sac by the filament *b*, and the continuity of this with the vesicle *c*, are shown. Two rather large grumous masses occupy partly the apex of the sac.

Fig. 8. Embryonary sac, a good deal more advanced. The upper part (except the apex itself) is now subdivided into a good many cells, almost all of which present a nucleus, all being crowded with grume and containing some granulcs, particularly those in which the nuclei are not evident. The formation of the cells is extending downwards, the basc of the sac alone presenting its original membranous hyaline appearance. At *a*, the perforation of the sac is seen; the continuity of the vesicle *b* (which has undergone no change) with the filament *d* may also be observed. The peculiar manner by which the uppermost series of cells of the sac have commenced, extending, as it were, over the lower edge of the vesicle, is also observable.

Fig. 9. Apex of an embryonary sac, more advanced, after the action of nitric acid. The vesicle, which is plainly continuous with the protruding filament, now contains many nuclei.

Fig. 10. Seed from a young fruit $1\frac{1}{2}$ line long. The apex of the original embryonary sac is now nearly concealed by the encroachment of the cells or young albumen. The opake spot *a* represents the embryo, which would hence appear to occupy the situation of the original vesicle.

Fig. 11. Longitudinal section of a more advanced fruit. The viscous tissue does not yet extend around the central tissue and its *horns* or filaments. The embryo is now oblique.